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# Social Dynamics in Populations of the Great Tit, Blue Tit and Marsh Tit

By

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**Abstract.** The composition of the nesting populations of the great tit *(Parus maior)*, the blue tit *(Parus coeruleus)* and the marsh tit *(Parus palustris)* are different. The number of the nesting individuals immigrated from foreign associations is highest in the population of the great tits and lowest in that of the marsh tits. (The proportion of the individuals hatched within the association and nesting there is lowest in the population of great tits and highest in the one of the marsh tits.) In this respect the blue tits take place between the two other species. Among the three related species the population density of the great tit is the highest and that of the marsh tit the lowest. This is the reason why the social repelling effects operate intensively in the associations of the great tit, and why their operation is weak in those of the marsh tit; similarly, this accounts for the extremly differing mobility of the two species, as well as for the dissimilar composition of their nesting populations.

It is the social repelling factors that induce the process by which a species enters new adaptation areas. Social selection forces the young individuals, mainly on the lowest levels of social structure, to an unfavourable ecological environment where they have to adapt to the living conditions.

The great tit is a species well adapted to urban and industrial environment, the marsh tit, on the other hand, is not. (Also in this respect the blue tit takes an intermediary place.) It is the intensive social repelling factor that forces part of the great tit individuals to settle (and to nest) in the urban ecological milieu that has originally been alien to the species.

The population dynamics need to be examined in the first place in the species which, on account of the high number of their individuals, have a significant part in the material and energy exchange of the ecosystems. For this reason researches often chose the great tits for elucidating by them population dynamic events. Artificial settlement of nestboxes enable them to survey a great number of nests in a relatively small area, so that in this way studies of breeding ecology founded on detailed analysis could be achieved (Balen, 1970, 1973). Artificial settlement of nestboxes promoted the study of the density determining role of food supply (Gibb, 1957, 1960, 1963), as well as the investigation of the correlation between the age and size of the territory (Dhondt, 1968, 1970). Besides these, numerous studies were published, which reported on the factors regulating the

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density of great tit populations and the effects of these factors (LACK, 1952, 1966; KLUYVER, 1953, 1957, 1963, 1966, 1970; KREBS, 1970, 1971; PERRINS, 1965).

My investigations on the great, blue and marsh tits connected with the researches mentioned above, as they contributed to the full knowledge of these typical species of Europe, and gave at the same time information differentiated according to Hungarian conditions. My purpose was (1) to examine the part of social structuration in the population dynamic events and (2) to compare the three species of tits in this regard.

## Method

So that I can follow with attention the part of social structuration in the population dynamic processes, I had to find a relatively isolated community of tits, within which the individuals of the population maintained contacts with one another in visual or acoustic way. It was necessary, further, that this system of connections should be interrupted beyond a certain limit, and that a lack of contacts should come about which surrounded the community maintaining the contacts and separated it from the neighbouring communities like an island. This is, namely the way in which a relatively closed association is formed, and its isolated life can be studied.

Complying with these requirements, I had to choose an area where the optimal habitat of three tits species was surrounded by a scanty ecological district in a ring-like manner. Namely, the tits settled in the zone of poor ecology can only maintain contacts mainly with individuals living in the central (ecologically advantageous) area, and become this naturally isolated from the neighbouring communities. For the investigations I chose an area of 400 hectares in the oak forests (the typical forest stand of Hungary) in the environs of Budapest. The best habitat of the area was formed of the edge of a 40—50 years old Quercus petraea stand near arable fields with a wide long ditch on 20 hectares. It was the district that ensured the most varied food and the the most suitable nesting area (numerous natural holes) for the tits (noted: district *A*) Inside of the *Quercus petraea* oak forest extenden on about 100 hectares, as an area of medium ecological quality (noted: *B*). All this was surrounded by a several kilometres wide karstic shrub forest, consisting for the most part of scattered Austrian oaks (*Quercus cerris*; noted: *C*). Of this district I chose 280 hectares for the investigations, in a manner that it should completely enclose the inner area of higher ecological value. For expediting examination, I also set up an artificial settlement including 200 nestboxes, which extended over certain parts of the three ecological districts.

In order that I could follow with attention the inner life of the community of tits, I also had to watch the movements of the individuals from place to place. This was only possible if I previously marked the individuals with coloured rings, and then permanently identified them in their habitats. However, owing to the rich vegetation, the observation of the individuals and a close follow up of their movements would not have been possible excepting in the winter seasons. Still, by playing back acoustic signs through a tape recorder I attracted all tits of an

area of 150 – 200 metres in diameter near the loud-speaker, and there their individual identification did meet with difficulties any more. I divided the whole area of the investigations into districts corresponding to the range of attraction of the loud-speaker, and in this way I was able to survey the location of the individuals with topographic accuracy. There were 72 sites of survey of this kind and, according to the time at my disposal, I conducted investigations in 10 – 25 of them in a day.

The most suitable acoustic sign of attraction I found in the course of experiments. The tits were attracted most by a continued repetition of anxiety churrings lasting for 2 seconds, at intervals of 1 second. I measured the 150 – 200 metres area of audibility similarly by means of experiments. Near their nests and at the winter feeding places the birds stayed in the same place on several occasions. When determining the range of reaction, I sounded the loud-speaker at various distances from the tit staying at one of such selected points and listened to the response of the tit. By changing the place of the loud-speaker (carryng out the experiment with several individuals) in this way I was able to determine the range of the anxiety call (within a radius of 70 – 100 metres).

The use of the acoustic attracting signs was of help also when I ringed the birds, because I could catch the individuals approaching the loud-speaker with a net. Still, a significant part of the markings I did as early as at the birds' nestling age, and in winter, in the neighbourhood of the artificial feeding places. I set up artificial feeding places in 15 – 20 points of the studied area, mainly in order that, relying upon the interindividual conflicts taken place in their vicinity, I could find out the sub- and superordination relations of the encountering individuals.

Broken down to each of the mutual effects it was impossible to find out the relations of sub- and superordination, still the social stratification within the association became clearly outlined. In its basic features, this social stratification reflected a hierarchy by age of life: the 3 – 5 years old individuals represented the highest stratum — further on mentioned as $\alpha$ individuals, — and the 2 – 3 years old ones formed the middle stratum — further on called: $\beta$ individuals. In general, the 1 year old individuals represented the lowermost stratum of the social structure together with some 2 – 3 years old individuals thrust into the background in spite of their older ages (further on: $\gamma$ individuals). (In the Table presenting the social structuration and the dispersion I noted the population's own 1 year old generation by a special sign.) In consequence of their relation to the "indigenous" members of the association, the individuals which had come from foreign parts were confined to the lowermost social stratum and their subordinate relation came to an end only after a 1 – 2 years' time of acclimatization.

I started the investigations in 1966, however, an adequate picture about the social structure of the population was formed only by 1969. Thus, regarding the social dynamic processes I could make authentic findings only from 1970 on.

In the course of the investigation lasting for ten years I could observe a recurrence of the social dynamic events. This permitted me to outline a general picture to be considered a model, in which I could place all concrete social dynamic processes and also the factors influencing them. Since this model serves as a directive for the discussion of the concrete social dynamic events, prior to entering into the details of the actual processes, I shall present it here in brief.

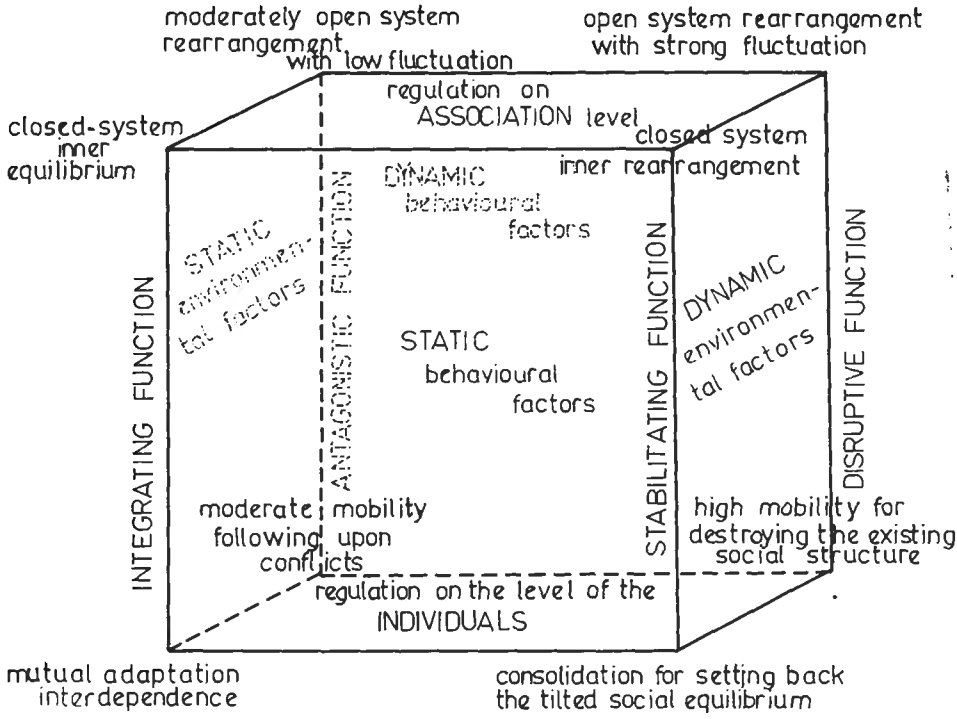



Fig. 1. Model of the functions of communication

**The model of functions of the communication regulating, the dispersion and social structure of the tit populations, relying upon the social behavioural and environmental factors**

The populations' constituent elements are the individuals. The individuals are integrated into a higher structural unity: into social unity by communication. Consequently, *communication is an inner regulating tool of social organization*. Communication, regulating the life of an association operates at all times in a joint effect of the individual interactions and environmental conditions. consequently, when determining the different functions of communication, one has to consider (1) the behavioural relations among the individuals and (2) the environmental factors.

The two groups of factors are divided into further two categories which, precluding one another, fit together in cube-form as follows (see Fig. 1). The upper surface of the cube symbolizes the whole of the association living together, its base the individuals forming the elements of the association. Out of the surface standing opposite of the cube, two stand for the interindividual interactions. the other two for the environmental factors. The period when the social connections maintain unchanged interindividual relations is represented by the *static* side of the cube, again, the time in which the interindividual interaction call forth a transformation of the existing relations is symbolized by the *dynamic* side of the cube. Consequently, one differentiates between static and dynamic

factors. Also the character of the effects of the environmental factors can be summed up in these two antagonistic factors. When they do not disturb the consolidated social equilibrum, they act as *static* factors, and when they change, they exert as *dynamic* effect. The other two sides of the cube are opposed to one another accordingly. The edges of the cube stand for those functions of communication, which are in the interaction of behavioural and environmental factors. The upper ends of the edges of the cube indicate the effect of the functions of communication exerted on the *whole* of the association, the lower ones show the direct effect exerted on the relations among the individuals.

Let us discuss one by one the functions of the communication under the effect of the various interacting factors, relying upon the model.

*a)* At simultaneous effects of *static social behavioural* and *static environmental* factors an *integrating function* regulates the intrapopulation connections. This function of communication expresses the interdependence of the members of the community, the adjustment of the individual to its direct social environment. By the scope of their activity and by their location, the individuals do not interfere with the actions and range of motion of one another.

In this phase the association is at rest, in a state of equilibrium. The ecological conditions meet the demands of the association, the members of the community may satisfy their needs in compliance with the internal arrangement. In this phase the community can be considered a closed unit, since the population is not decreased by individuals streaming out, neither increased by the entry of new ones. Since all factors affecting the life of the association approach the optimal level, the density of the population is in keeping with the carrying capacity of the area; indeed, a part of the given ecological possibilities even remains unutilized.

*Thus, in consequence of individual adaptation and mutuality, the association is characterized by an internal eqilibrum of closed system at the integration function.*

*b)* When *static environmental* and *dynamic social behavioural factors* interact, an *antagonistic function* regulates the community. The ecological conditions are unchanged, and although they would satisfy the demands of the association also in the future, the mutual adaptation of the individuals comes to an end. On account of their new drives, the birds need a new district of activity, which they can achieve only by transforming their social connections. The number of encounters between the directly interacting individuals increase, and this manifests itself in considerable mobility.

If at the time of the rearrangement the association has adequate ecological reserves at disposal, then the transformation passes off as an internal process of the community. If, on the other hand, the ecological conditions are insufficient for the modified demands, then a part of the individuals leave the community, i. e. in such instances the closed character of the association comes to an end. At other times the antagonistic function completely breaks the social bonds connecting with the community, in spite of the fact that the essential conditions would be ensured by the unchanged ecological factors. Consequently, certain emigration begins also in such cases. An exclusively closed system is out of question in that period anyway, since even if rearrangement happens as an "internal affair" of the association, guests may arrive from the neighbouring

associations which, in consequence of the antagonistic effects prevailing there, fly across the isolation area which separates the associations, and temporarily or permanently settle as newcomers. In actual fact, it occurs but seldom that, as a result of the antagonistic function, the association would not be joined by new individuals and left by some which belonged to it.

*Consequently, during the antagonistic function the population is characterized by a restratification of moderately open system, and, as a consequence of the multiplication of the individual discords, also the mobility of the individuals in increasing at that time.*

*c)* When *static social behavioural* and *dynamic environmental* factors interact, it is the *stabilitating function* of the communication which is existing. The biological advantage of living together is best reflected by this function: a social organization of the individuals harmonically fit into the community. At such times the individuals establish still closer mutual links, and compensate the changes that could be destructive to the social system. By mutual adaptation to the intensified social restrictions, the individuals do not only ensure their own survival, they also guard their social unity against the loosening factors of external origin.

With the deterioration of the ecological conditions, the association loses its equilibrium upon their effect; still, parallelly with this an inner rearrangement consolidates the unstable system of interactions. Upon the effect of stabilitating communication the state of equilibrium is, as a rule, reestablished by an increased concentration process, (by an increased density of population in certain districts. Without a break in the closed unity of the association, the community continues to utilize the decreased carrying capacity of the habitat.

Summing up the above: *during the stabilitating selfregulatory process, in consequence of the consolidating efforts of the individuals, an inner restratification of closed system takes place.*

*d)* When *dynamic environmental* and *dynamic social behavioural* factors interact, social communication performs a *disruptive function*. Upon the joint effect of changing environment and altered social tendency the communicating individuals turn against their community. They break with the social milieu in which they have lived till then. Upon the effect of repeating aggressivity the following reaction becomes weak, and the social facilitation leading to common activity does not function either. The individuality is highest and antagonism among the individuals is keenest.

Since the ecological changes coincide with the modification of the social behaviour – independently of whether the ecological changes are advantageous or detrimental – the most dynamic transformation of the population's life happen at that time. The community gets into an exceedingly mobile condition and the structure preaviling up till then is broken up by the considerable rearrangement. By destroying the existing social structure, the disruptive function prepares a new structure, and this dynamical state also opens a way to the neighbouring associations. Among the more or less isolated associations an intensive exchange of the individuals takes place, and such inter-association relations last until the environmental factors are stabilized, and social connections are balanced once more. Eventually, the social structure is completely transformed and to some degree also the neighbouring associations take part in this process.

*Thus, the individuals strive, with their high mobility to decompose the existing social structure during the disruptive function. At such instances an open-system regulation takes place, in the course of which also structure-forming elements (individuals) of external origin take part in rearrangement.*

Let us discuss one by one the functions of the communication acting through an interaction of the various environmental and social behavioural factors, relying on the model.

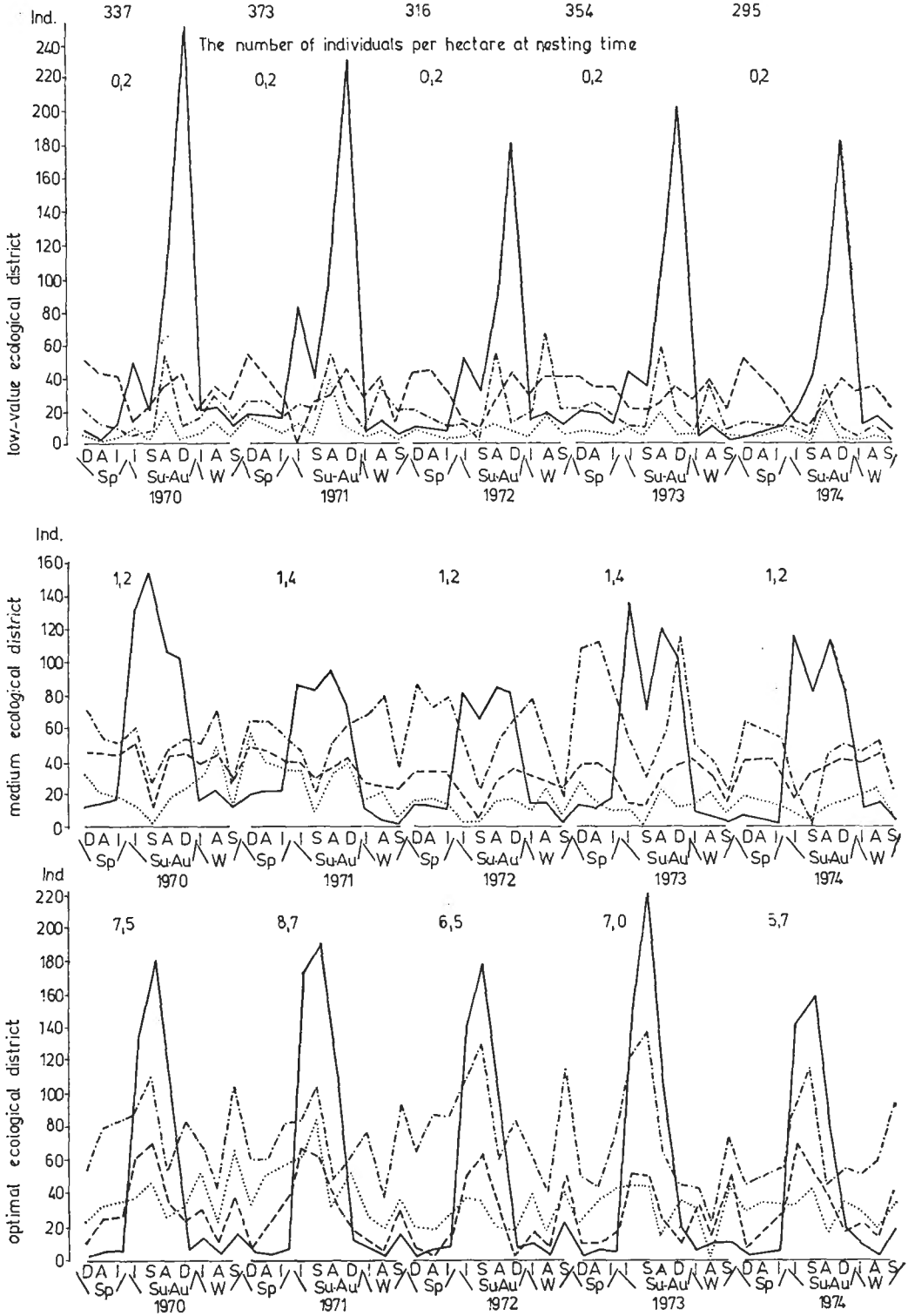
## The regulating functions of the communication in the yearly life period of the tits

The alternation of seasons divides the yearly life cycle of the tits into three separate periods: (1) the spring, territorial period, (2) the summer-autumn period (the one of rich vegetation and food supply) and (3) the winter period. In the course of the investigation my aim was to obtain data by functions on at least 5 occasions in all three periods of each year from all points of the studied area. This minimum objective I could easily realize, and was able to take even 5 – 10 surveys of the situations on same points. In the Figs. 2 and 3. I indicated the mean values resulted by the surveys. By means of these one can find out what the dispersion of the population was like in the various areas and what restructuration processes took place during the change of this dispersion while the various functions existed. Still, for a detailed representation of the social dynamics only the populations of great and blue tits were suitable (Figures 2. and 3). In the populations of marsh tits of which the density is low, the social changes are realized, namely, with few individual translocations and therefore the social dynamics of this species differs from the one of the other two tit species. Consequently, also their discussion needs to be separated from those of the great and blue tits.

### *The regulating functions of the communication in the territorial season*

#### *1. The disruptive function*

The beginning of the nesting period is indicated by an increased demand for space of the individuals (and pairs, respectively): the aggressive tendecies abruptly increase. Parallelly with this a rapid transformation takes place also in the environment. (Temperature rises, the days grow longer, the vegetation and the insects revive.) At the time of disruptive communication the groups more or less concentrated in winter break up and are dispersed by pairs over the area inhabited by the community. The unevenness of the dispersion is conspicuous. The density of district $A$ is especially high in comparison with those of district $B$ and $C$. The $\alpha$ and $\beta$ individuals are dispersed in approximately equal quantities in district $A$ and $B$ (the district $A$ is five times smaller than district $B$!). The $\alpha$ individuals enter district $C$ in insignificant numbers, on the other hand, the $\gamma$ individuals, the ones of the community's own raise which breed for the first time are insignificant in district $A$.


The number of individuals in the whole area of the examination /on 400 hectares/at nesting time
337
373
316
354
295
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The number of individuals per hectare at nesting time
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low-value ecological district
1,2
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medium ecological district
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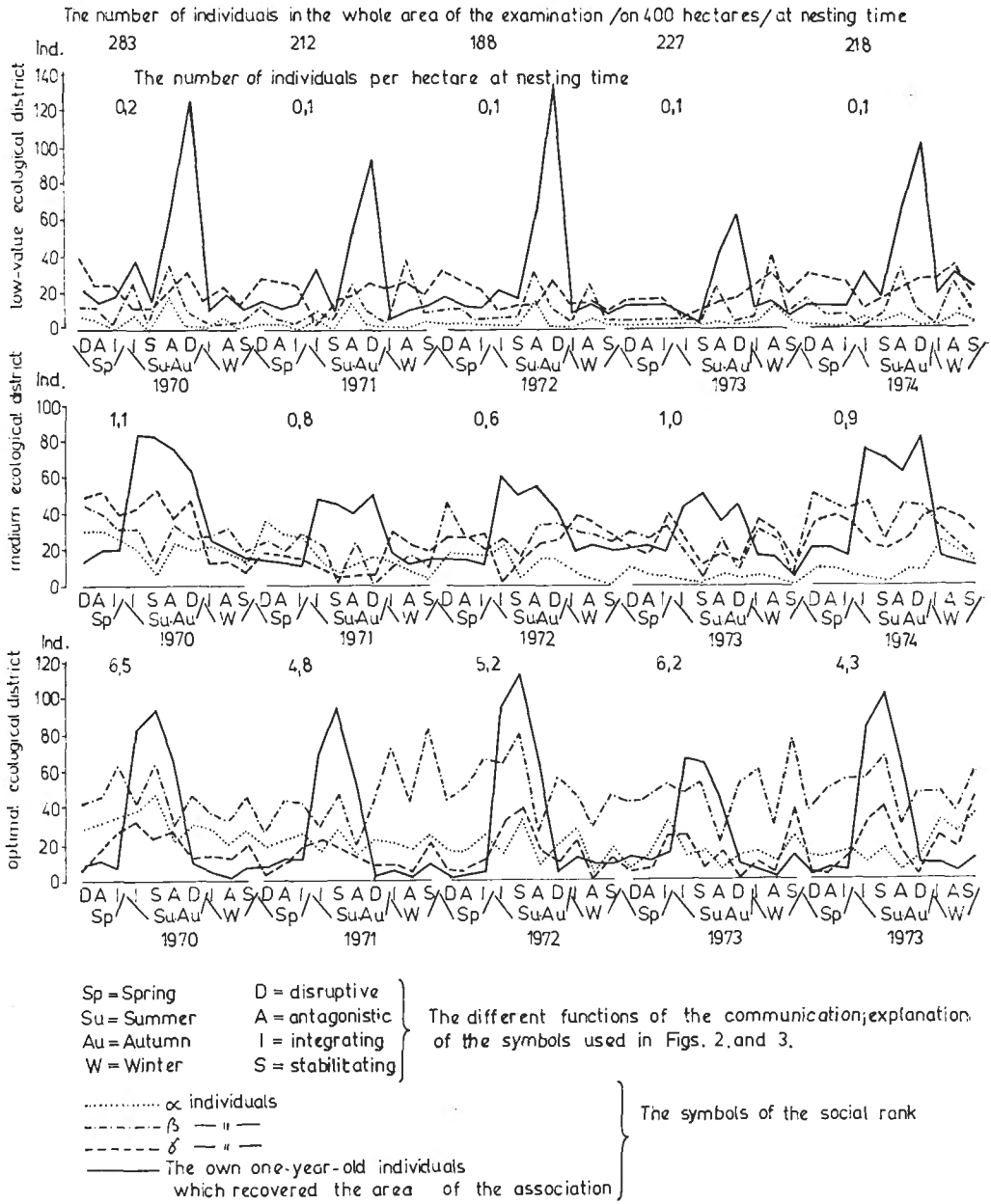


Fig. 3. Dispersion of the blue tit due to different functions of communication

◀ Fig. 2. Dispersion o the great tit due to different functions of communication

### 2. *The antagonistic function*

By the time when the wide weather fluctuations of early spring have stopped, the behaviour which as an inner contradiction of the association, holds the individuals off each other, continues to act. An arrangement more dispersed than that in winter still characterizes the population, however already in a smaller degree than at the time when the disruptive function was existing. Consequently, in this period concentration to district *A* (of optimal habitats) somewhat increases as compared to disruption. (In general, the numbers of $\beta$ and $\gamma$ individuals increase in district *A*.)

### 3. *The integrating function*

The members of the community have divided the nesting area among each other. (This division began with the disruptive function.) Between the nesting pairs a stable connection has formed. (The acoustic guarding of the territories, at the same time, connection among the neighbouring birds by acoustic means.) The processes of rearrangement have come at rest. When comparing the dispersion with the one to be observed with the antagnonistic function, one can find that the density of individuals contiuned to decrease in district *C*. It were mainly the $\beta$ and $\alpha$ individuals which moved to the central area.

In most part of the nesting period the integrating communication is functioning. Concentration to the most suitable ecological districts is clearly indicated by the proportions of settlement. If one combines districts *A* and *B*, which amount to 30 % of the total area, then one can see that 85% of the great tits and 82% of the blue tits breed there, and the remaining $15-18\%$ are dispersed in district *C*: in 70% of the whole area covered by the spread of the association (mean values of 5 years). The specific social structures characteristic of the district illustrate the ultimate result of the function of the communication in the period of nesting, i. e. the end of the rearrangement which took place in that period under the regulating function of the communication. In that process the majority of the individuals of high rank occupied the best nesting areas, and even most of the $\beta$ individuals found place there. The bulk of the $\gamma$ individuals nested in the medium area, still at the same time a considerable part of them was only able to settle in district *C*.

### 4. *The stabilitating function*

At the beginning of the breeding period I could observe in some instances that when the male which had disposed of an own territory and a more or less completed nest died (probably fell victim to predator), his place was taken by another male individual. The territory of the missing male was in a favourable ecological district, and the newcomer had possessed a territory in a peripheric and inferior ecological zone. The newcomer also brought along his mate.

After the male who used to be the owner of the territory had disappeared, no song was to be heard any more from the district left empty and this announced the release of the area for the surrounding birds. The neighbours nesting among

worse circumstances could thus settle in the favourable nesting area which had become unoccupied and, following some exploratory visits, one of them actually did so. In this way, within the system of territories bordering on one another vacant sites existed only temporarily. The community ensures a concentration to the most suitable area and its fullest possible utilization through the interindividual connections (by means of the territory songs). In some kind of a disorder ensules in the already established arrangement, the community consolidates the condition which existed prior to the trouble; e. g. it resettles the area depopulated by predator. (Naturally, this cannot happen at an advanced stage of nesting, because then the tits do not part with their territories any more.)

*The regulating functions of the communication summer—autumn season*

*1. The integrating function*

When the territorial period has concluded, the longest period of rest begins. The life of the community is determined by stable environmental factors and balanced social connections even after the young birds have become independent. The spring integration period which includes the hatching and raising of the nestlings and the summer integration period are continuous. The population is considerably increased by the accession of the new generation: late in July and early in August the number of the young birds approximately agrees with that of the older individuals.

Comparing the summer integration period with the spring one can find that the proportions of dispersion have essentially not changed in the three types of areas. Also the dispersion of the young is basically determined by their birthplaces, and although they move in a wider district than was the territory of their parents, they do a great part of their daily activity in the area where their parents have chosen their nesting places. The greatest change appears in the high mobility of the $\gamma$ individuals, their numbers considerably increase in the central district $A$.

*2. The stabilitating function*

In summer, the cold spells lasting several days evoke a concentrating process. The birds take shelter mainly from the wind and find areas for this purpose in the central district $A$: bottom of valleys and ditches. Social coherence gets stronger, the following reaction intensifies, and at times also mixed groups of the great, blue and marsh tits are formed in district $A$. The density of district $B$ and $C$ decreases.

*3. The antagonistic function*

Following the moulting time the association's period of rest comes to an end. The social dynamic effect of reviving territorial behaviour is high, although by far not so strong as in spring, since also the new, generation takes part in

the autumn territory skirmishes. Thus the integrational unity of the association breaks up and, as a consequence, scattering increases. The density of district *A* decreases. As a result of the territory skirmishes certain emigration begins, in the first place from the young individuals born in spring and from the $\gamma$ individuals.

### *4. The disruptive function*

Together with the instinctive drive which forces the individuals to increasing mobility, the autumn turn of seasons, radically changing all factors of ecological environment, gives rise to the most dynamic period of the association. With the gradual deterioration of the living conditions, the individuals draw towards the central district (*A*) where they find more food and relative protection from the rigid weather. Numerous individuals accumulate then in a small area where mutual tolerance is becoming continually lower. Upon the effect of intensifying social repelling part of the individuals – mainly the lower two strata – leave the central area in a short time. On account of their mobility, the young and $\gamma$ individuals, namely, seldom enter in repeated fights on their meetings with older individuals. This rapid departure can also be ascribed to the circumstance that the transformation of the environment is gradual and, especially at the time when the disruptive function is existing, not even the peripheral ecological conditions deteriorate to a degree where they would prove quite unsuited for supporting the tits. Thus, the individuals exposed to continuous attacks found food far from the central area, and leave easily the area of the whole local population.

In spite of the disruptive effect, in the central area one finds a growing concentration, however only on the part of the $\alpha$ and $\beta$ individuals, since the numbers of the $\gamma$ individuals and of the young ones decrease. This clearly demonstrates that in the processes of rearrangement social "status" has a decisive role, since the individuals of high degree of rank increase the rate of their participation in the areas of best ecological potentialities and drive those of lower ranks out of there. Consequently, considering the whole of the association – also including the young individuals – a vast deconcentration takes place during disruptive communication. The quantity of the youngs indicated in area *C* on Figures 2 and 3 means mainly the number of the individuals leaving the association, which departed through area *C* without having stayed in the peripheral area as actual structure-forming elements or strata. The majority of the young individuals, namely, passed through that area rapidly and without longer stay, only few of them spent a shorter or longer time there.

## *The regulating functions of the communication in the winter season*

### *1. The integrating function*

The part of the tits in the material- and energy exchange of our forests obtain increased significance especially in winter, when their numbers as compared with those of the individuals of all bird species are highest. In spite of the deteriorated living conditions, during the integrating function the dispersion of the

population is consistent with the ecological conditions; accordingly the connections of the individuals ensure an optimal arrangement of the association.

The dispersion of the individuals within the area clearly reflects the association's hierarchical order. The majority of $\alpha$ and $\beta$ individuals stay in district *A*, in district *B* and *C* their quantity decreases. The $\gamma$ individuals and the majority of the young ones find place in district *B* and, at times, *C*. (The dispersion of these two social strata in fluctuating, in certain instances their numbers are lowest in district *C* in others in district *A*.)

### *2. The antagonistic function*

On mornings late in December and in January the integrating connections are interrupted, the groups staying together are breaking up, and in consequence of all this the population disperses on a wider area. The aggressive skirmishes and the repeatedly sounding territory songs denote the revival of territorial behaviour.

In consequence of the spread of the association the number of individuals is increasing mainly in district *B*, still, in spite of their dispersion, the majority of the $\alpha$ and $\beta$ individuals remain in district *A*. The majority of $\gamma$ individuals takes place sometimes in district *B*, sometimes in district *C*. The dispersion of the young birds is relatively steady even at that time, although they stay in somewhat greater numbers in district *B* and *C*.

These antagonistic processes, however, are rather temporary. The individual skirmishes are weak and infrequent, neither is scattering significant. Consequently, the association invariably preserves its close character, and no emigrating occurs either. By the afternoons even this loosening comes to an end, and the social connections become closer once more.

### *3. The stabilitating function*

At the time of the territorial dispersion, as well as in autumn one could equally observe that stabilitating communication performed the association's most important function of selfdefence. Using a cybernetic term: stabilitating function is a communication form of negative feed-back, by which the tilted social system is set back in a state of equilibrium. This regulating process acts during the unfavourable ecological changes in winter, the social attraction becomes stronger, and upon its effect also the individuals staying in the periphery get among more favourable living conditions. In this way also the subordinate individuals find areas richer in food and more free from the rigours of the weather.

Concentration is the most intense in this communication, both in district *B* and *C* there are few individuals staying. In district *C* the share of the older birds attained not even 10% in the majority of the cases. District *A* was entered by the $\gamma$ individuals in the least degree. As a rule, these stayed at the peripheries of the large mixed flocks (together great, blue and marsh tits), and in the course of moving in groups, they were often left back in district *B*: moreover, at times even in district *C*. With the $\beta$ and $\alpha$ individuals this was less frequent.

*4. The disruptive function*

During the winter disruptive communication the association passes through its most critical period. The suitable habitats are narrowed down by the deterioration of the ecological factors to an extent where overpopulation ensues in them. Sometimes the $\gamma$ individuals and the young birds cannot even satisfy their minimum demands for food since, upon the skirmishes they are driven out of the overcrowded district *A*. (More correctly, only of certain parts of district *A*, where the adequate living conditions have continued.) For all that, they do not leave the association, since the probability of survival would be even lower if they moved too far from the district offering minimum chances of surviving.

However, the critical situation evoking the disruptive function seldom ensues in our plains and hilly regions. The tit populations tide over the short grave periods of the mild winters characteristic of our climate by means of the stabilitating communication. Not once in 10 years could I observe in the areas I studied that tit communities living together would have suffered considerable losses on account of the worsening living conditions. (That is the reason why disruptive function is not included in the Figures.)

**The composition of the nesting population of the great and blue tit**

The inner motion of the associations has two main directions: one of concentration and another of deconcentration. In a state of rest, integrating communication maintains an unchanged structure at unchanged dispersion, and subsequently to this either a tendency of dispersion ensues on the effect of the antagonistic but especially of the disruptive communication, or, contrarily to it, concentration ensues upon the effect of stabilitating communication. If the disruptive function is followed by antagonistic function, then in proportion with the strong dispersive effect of disruption — in spring, at the time of territorial dispersion — some concentration takes place, otherwise (in autumn and in winter) following the integrating function it evokes deconcentration.

Upon the effect of the antagonistic and disruptive communication part of the individuals of the community leaves the association; still, since the same phenomenon takes place also in the neighbouring communities, the individuals which have left there, arrive in the association. The composition of a population is determined at all times by the numerical relation of the progeny of own raising and the individuals come from foreign parts and settled there, as well as of the individuals which had died or left the association. The question was whether there was a culmination period, when the nesting composition of the population was formed, and if there was one, in what time did it fall? The investigations of KLUYVER (1966, 1970) on great tit populations demonstrated that the breeding stand of this species was formed as early as at the end of autumn. By the way, with this statement KLUYVER also took stand in the debate of WYNNE-EDWARDS (1962) and LACK (1966), in favour of the former. In WYNNE-EDWARDS's opinion, namely, aggressivity prevailing among the individuals in autumn decreases the population to a degree that later it can already endure the decrease in food supplies, and the survival of the individuals is not threatened any more. On the other hand, LACK considers the direct struggle for food the factor (mainly in winter) regulates the size of the population.

I carried out joint studies in great and blue tits, and relying on them I have to agree with statement of KLUYVER and WYNNE–EDWARDS. During the summer integration period, lasting from about mid-June to about mid-August the proportion of the youngs – as also to be seen in the Figures – approximately agrees with the number of adult individuals. If, following this, we examine the data of integration in winter, the majority of which I took during December and the first part of January, we can see that the proportion of the young birds has fallen to a low level. Further, if we compare the data of the winter integration with those of the spring one subsequent to it, we can state that also the dispersion and social structure approximately agree with one another. In the years of the investigation discussed here – characteristically of the hilly and plain regions of Hungary – there was no lasting cold weather, and thus the population in autumn was able to live through the winter months without adversities. Even from the districts of lower ecological value the tits withdrew but very infrequently and for few days to the centre at the time of stabilitating communication. The considerable dispersion taking place early in spring was already modified also by the antagonistic communication, and since each individual strove to reach the best breeding area, by the time of laying eggs the dispersion characteristic of the winter integration was almost completely restored – however, this time already with territorial separation.

KLUYVER (1966, 1970) ascribes the autumn fluctuations to the territorial behaviour prevalent at that season. In the autumn fights for territory also the youngest generation hatched in spring takes part, and it is in the first place this generation (the individuals of lowest rank) which is driven out of the community. Also the change in the weather at the end of summer and in autumn by which the birds are gathered in small crowded districts, have an intensive disruptive effect. In these narrow districts part of the association is forced by the recurrent skirmishes to leave the area inhabited by the population. Still, the autumn fluctuation may be brought about in the first place by the circumstance that, on account of their inner drives, the individuals are much more mobile at that time than in other periods. This holds especially for the young birds which stayed only for a few months in the neighbourhood of their hatching place, and the endeavour to adhere to one area has not yet been formed in them. (It will be strong in them only after the first breeding.) This internal instinctive mobility is maybe related to the drive which starts the movements of the migratory birds, still, for these migration to long distances is made necessary by ecological conditions having their roots in the evolutional past. The species adapted to the winter conditions, thus the great and blue tits, are not forced by the change in the weather – and of all factors of the environment along with it – to cover long distances. Their mibility only induces them to cover relatively short distances.

That the population formed in autumn survives unchanged, is also supported by KREBS (1971). He found that the artificial feeding in winter of the great tits did not effect the density of their breeding density, and also among blue tits he could observe a phenomenon of this kind only on relatively few occasions. In this opinion the spring territorial arrangement of the birds serves mainly the purpose of delimiting the pairs from one another and of establishing the place occupied for breeding and not that of regulating the density of the population.

KLUYVER (1966, 1970 *a*, 1970 *b*) examined a well-isolated population of great tits in the island of Vlieland in the Netherlands, and found out what percentage of the breeding population was formed each year by the population's offspring of own raising. He proved by experiments that if the population of great tits had been befallen by a heavy loss, then the diminished numbers were completed mainly by the population's own stand; partly through a decreasing mortality of the older individuals and partly through a reduced measure of emigration of the younger ones. In the course of investigations, I surveyed in six successive years the proportion of the population's breeding individuals of own raise and of such individuals having arrived from foreign community since the last breeding season.

*Table 1. Percentual proportion of the one-year-old breeding individuals (which recovered the area) and the breeding individuals come from foreign associations in the great tit population*

| | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 |
|---|---|---|---|---|---|---|
| One-year-old breeding individuals which recovered the area | 7 | 12 | 9 | 10 | 7 | 11 |
| Breeding individuals come from foreign associations | 17 | 26 | 21 | 23 | 20 | 24 |
| Those which bred firts in the association, altogether | 24 | 38 | 30 | 33 | 27 | 35 |

*Table 2. Percentual proportion of the one-year-old breeding individuals (which recovered the area) and the breeding individuals come from foreign associations in the blue tit population*

| | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 |
|---|---|---|---|---|---|---|
| One-year-old breeding individuals which recovered the area | 12 | 14 | 15 | 14 | 11 | 15 |
| Breeding individuals come from foreign associations | 13 | 16 | 20 | 18 | 18 | 16 |
| Those which bred frist in the association, altogether | 25 | 30 | 35 | 32 | 29 | 31 |

If one compares the data summed up in Table 1 with those of KLUYVER (1970, p. 519). the most conspicuous difference to be noticed is that in the breeding population examined by him the proportion of the one-year-old individuals is much higher than in the breeding population studied by me. In the island of Vlieland 50% of the breeding population consisted of one-year-old birds and. following the experiment, when in the preceding year that author had decreased the number of the youngs by 40%, the proportion of the one-year-old individuals was 36%. In the Hungarian population the one-year-old breeding individuals which recovered the hatching area together with the breeding individuals coming from foreign parts attained the proportion characteristic of the experimental years in Vlieland. I could make essentially the same findings also in respect of the blue tits. The majority of the great and blue tit populations consisted of the

$\beta$ individuals including the 2–3 years old breeding ones. The $\alpha$ individuals were mainly the 3–5 years old birds of the population's own raise. In no instance could I perceive a 6-years-old brooding individual.

The higher proportion of older individuals can be explained presumably by their higher values of survival, and by emigrating of more young than it was in Vlieland. Namely Vlieland is an isolated island and the area studied by me is not a well-separated district from the forests covering the hills continously near the Budapest. The youngs and the individuals arrived from foreign populations could fly easily away from this area by the attacks of the adult tits. It is the mild winters and maybe the higher autumn mobility of the youngs in this country which cause the higher recovery of the older birds, as well as also their increased participation in the breeding population. Still, apart from this common feature, the great and blue tit populations also differ from one another in this respect. The young blue tits, namely, take a greater share in the breeding of their own association, than do the young individuals of the great tit in the one of their own, and vice versa: in the great tit population the individuals come from foreign populations nested at all breeding times in higher proportion than in the blue tit population. Consequently, the great tit is a more mobile species than the blue tit; i. e. the reason why more individuals from foreign parts can permanently join the great tit population is that there are more which leave it, and less individuals can join the blue tit population, because the proportion of the birds staying there is higher. (Their association is, namely, more closed.) All this is presumably also related to the lower population density of the blue tits on account of which also the conflicts within the association are kept on a lower level than with the great tits. The investigations of BERNDT and STERNBERG (1968) supported the fact of an adherence of the blue tits to their birthplace.

Spring integrating communication connects the individuals of the association during the balanced and stable period of the nesting population. The fluctuation of the bredding population can be surveyed clearest in the optimal district, since the tits populate districts *B* and *C* but scattered, and in the extensive areas the changes in their density remain unnoticed. In the succession of years the numbers of individuals per hectare hardly reflect the fluctuation of the population in district *B* and not at all in district *C*. Naturally, this means at the same time that in these districts the population's fluctuation is low. Namely, at the time of the autumn emigration and immigration, the majority of the individuals which have been forced out of the optimal area do not stay in the direct periphery but leave for farther areas. The number of the individuals remained in the community is determined in the first place by the interindividual relations prevailing in the centre. The influence of these affects the populations of the peripheral areas in so far as the individuals driven out from the centre, which adhere to their area and at the same time to their association, do not leave their community. The density of the peripheral areas remains, however, insignificantly low in comparison with that of the central area.

In the period between 1970 and 1974, the density of the best (*A*) breeding area was high. The average of the breeding pairs of great tits falling to one hectare surpassed 4 in 1971, the one of those blue tits surpassed 3 in 1970 and 1971. (So although the blue tits hold a smaller territory, their population density was lower than that of the great tits.)

The fluctuation of the population of the great and blue tits did not proceed parallelly, still at the same time no competition could be found between the two species either. In 1971, simultaneously with a rise in the density of the great tits that of the blue tits decreased, then, in 1972, with the decrease of the former that of the latter increased. In 1973, on the other hand, the number of the breeding individuals of both species rose, then in 1974, the ones of both became less. The niche of the two species, namely, covers each other only in part since the blue tit feeds mainly in the foliage and the great tit in the litter. Again, at nesting time the territorial behaviour of the great tits is favourable for the blue tits which search for holes. There are, namely, several suitable free breeding holes within the occupied territory of a great tit, which the other great tits cannot use because the possessor of the territory drives them away from there. Still, the great tit does not protect its territory (only its direct nesting hole) against the blue tits, and so these can occupy the holes left empty within the possessor's district of the territory.

In 1971 the rise of the great tits' population was caused on the one hand by an increased survivorship of the old individuals (the number of the $\alpha$ individuals had grown), on the other hand, also the proportion of the tits come from foreign parts and of the association's own individuals breeding for the first time increased. The relatively high decrease in population of the next year (1972) can be ascribed in the first place to the disappearance, presumably to a dying off, of mainly the $\alpha$ $-$, consequently of the aged individuals. The population increase of the blue tits in 1973, and following thereupon, their population decrease in 1974 can be explained by similar phenomena.

In the tit associations studied by me the second breeding often failed to occur, and even if it did take place, the number of the breeding pairs was very low. In the years 1970, 1972 and 1973 I could not observe any second breeding at all. In 1971 only a sixth of the great tits, a fifth of the blue tits, and in 1974 a seventh of the great tits and a fifth of the blue tits nested repeatedly. In the years 1970, 1972 and 1973 the youngs of the first hatch left the nests late, after June 1st, since the weather delayed nesting, and after that the parent birds did not begin breeding again. Relying on the examinations conducted at the studied area and even on observations made in other parts of the country I have to state that if the tits of Hungary have their first hatch leave the nests only after June 1st, they do not breed for a second time.

As the number of the repeatedly breeding pairs of tits was exceedingly low, the youngs which had left their nests did not essentially affect the density of the population. – Second breedings of marsh tits I could not observe in the course of my investigations lasting for ten years.

### The social dynamics in the marsh tit population

The social dynamics of the marsh tits differs from those prevailing in the two related species. Its peculiar character can be ascribed to the low population density of the species. Not even in their optimal habitat do the marsh tits form so continuous a community as the great or blue tits, they rather disperse over the area. Their territories are much wider than those of the great and blue tits, all the same, the males which are the possessors of the territory keep also connec-

tion with each other acoustically (mainly by songs). At nesting time 2—4 couples territorially separated from one another established together a small isolated association. There were 2—3 small isolated associations in the studied area, where the males could not keep connection with the neighbouring association by their songs because of the long distance. These smaller, separate association connect with one another mainly only at the time of the antagonistic and disruptive communications, i. e. in the period when their mobility is higher. However, the ecological district ensuring relatively a natural isolation of the tits (in the present instance an area of 400 hectares) is only exceptionally left by one or another individual. Owing to the low population density of the marsh tits there are no major "buffer effects" even in the optimal territory.

Thus the marsh tits are located in smaller associations within community of the great and blue tits. The slight fluctuation leading to moderate emigration and immigration falls exclusively on the time of the autumn disruptive communication.

On account of the low population density of the marsh tits I need not give as detailed a representation of their social dynamics as I did in the case of the great and blue tits; Table 3 and 4 reflect the social arrangement of this species only in the integration period of the breeding time. This arrangement essentially agrees with the social dispersion to be observed with the other two species of tits. The proportion of the one-year-old individuals from the population's own hatch and that the ones arrived from foreign parts I indicated both by absolute values and in per cent. The clearly demonstrate that in the marsh tit population the participation of the individuals of own raising is much more considerable than in that of the great and blue tits. We have stated that on account of their slighter fluctuation the one year old blue tits from their own community take part in the reproductive processes in greater measure than do the youngs of the great tits in the breeding processes. However, the young individuals remaining in the marsh tit population by far surpass the participation of even the youngs of the blue tit in the populating processes. When comparing the three species of tits with one another, one finds that it is the marsh tits which form the closest community.

## Conclusion

Following with attention the life of the tit populations we could find that each transformation induced by the ecological factors determined the dispersion and mobility of the individuals through the social relations. The population of the optimal district is determined by the carrying capacity of the area and by the interindividual connections; the effects of the limiting factors resulting from the interaction of the two influence the density of the peripheral areas. Depending on the proportion in which the ecological conditions are shifted towards the lowest values, these peripheral districts of lower carrying capacity are still suitable for supporting the species, consequently, part of the population exposed to the limiting effect of the central is able to settle here. However, the population of the peripheral areas is in almost every instance far behind the density, which the supporting conditions would permit in the majority of the yearly life cycle and naturally also behind the one made possible by the mutual tolerance

*Table 3. Dispersion of the marsh tits by their social rank and by the various ecological districts at nesting time*

| | | 1970 | | | 1971 | | | 1972 | | | 1973 | | | 1974 | | | 1975 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Social rank | | α | β | γ | α | β | γ | α | β | γ | α | β | γ | α | β | γ | α | β | γ |
| Ecological value of the area | optimal | 4 | 6 | 1 | 2 | 6 | 2 | 4 | 6 | 2 | 4 | 4 | 4 | 4 | 6 | 2 | 4 | 4 | 2 |
| | medium | 2 | 6 | 2 | 2 | 3 | 4 | 2 | 6 | 4 | 3 | 6 | 5 | 2 | 6 | 4 | 2 | 5 | 3 |
| | low | | 2 | 4 | | 2 | 2 | | | 2 | | | 6 | | 2 | 5 | 2 | 2 | 2 |

*Table 4. Number and percentual proportion of the one-year-old breeding individuals (which recovered the area) and the breeding individuals come from foreign associations in the marsh tit population*

| | 1970 | | 1971 | | 1972 | | 1973 | | 1974 | | 1975 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| One-year-old breeding individuals which recovered the area | 7 | 26 | 5 | 20 | 4 | 16 | 7 | 22 | 7 | 23 | 5 | 19 |
| Breeding individuals come from foreign associations | – | – | 2 | 8 | 2 | 8 | – | – | 2 | 7 | 1 | 4 |
| Those which bred first in the association, altogether | 7 | 26 | 7 | 28 | 6 | 24 | 7 | 22 | 9 | 30 | 6 | 23 |

conditions of the individuals settled here. Doubtlessly, the probability of survival of the individuals is lower in the peripheral area, because at times they are unable to escape from the degradation of the ecological conditions towards the cental area which offers more favourable possibilities of life, in wich, however, the density of individuals is high.

Consequently, the population dinamics is jointly determined by the ecological factors and social interactions. As we have seen when discussing the stabilitating communication, the social behavioural effects involve not only limiting consequences. The finding and utilization of suitable living conditions are facilitated by the social attracting effects. The settlement of the optimal areas, keeping the new generation in place and the admission of the immigrants arriving from foreign parts are realized through the positive connections between the individuals.

If the social connections were restriced only to mutual attraction then this would lead to the overpopulation to the optimal habitats and, subsequently to this, a mass destruction would decimate the population. Yet also those repelling factors are equivalent causes of the social connections, which drive part of the individuals to habitats of lower carrying capacity, and which in this way enable species to utilize also these areas (KLUYVER, 1953). Naturally, the adaptive capacity of the individuals driven out from thier primary community is severely pressed by the foreign conditions, and (apart from the fledgling time) the factors of selection are most effective in this period. Still, the individuals which have adapted to the new conditions may either begin to occupy a new ecological milieu, or continue to consolidate the expansion already begun.

Thus the social effects in a community are not necessarily concomitant with decline, quite the contrary, just in consequence of a situation extorted by the community it prepares a further step in the progress of the species. It is a negative effect upon the individual exposed to the selection of the community, which is not only advantageous but even indispensable for the survival and expansion of the species. If the social structure and within same the individual relation-system at all times preserved its closed unity, then there would be no chance of progressivity, consequently, the ecological valency of the species would narrow down and if this limited adaptive zone were hit by some drastic change, this would endanger the species living in it. Thus the species that has not endeavoured acclimatization in a new environment, preserves itself in a regressive condition without evolvement of its evolutional future.

A social ethological precondition of the expansion of species is that the associations should not form rigid, closed units and that they should at times open towards habitats untouched. As we have seen, the most mobile of the three species in this respect was the great tit, the blue tit passed less and the marsh tit least beyond the borders of their communities. The closed character of the association of the marsh tits can be led back to their low population density which, on the other hand, finds its explanation in their low value of survival. As compared with the great tits, their brood is less only by 2—3 eggs, and this does not give reasons why the density of the individuals of the great tit should be by about 15 times higher. The great difference is explained presumably by the high mortality of the marsh tit. The marsh tits, namely. do not adhere so much to covered and closed holes and caves as the great and blue tits. Out of the marsh tits living in the area of artificial nestboxes, at a time only one-two pair bred in

the nestboxes safety and protection, – the others, although there were at all times empty holes in their territory, used natural holes for nesting. Thus it can be understood that the rains in April and May destroyed a significant part of the broods. (The nests were often placed at forkings of branches or trunks where the water streamed in like in a gutter and soaked the eggs or the already hatched youngs.) The fact that the mechanism of the marsh tit's nesting instinct is not bound to a stimulus complex reflecting closed holes indicates the fixation of a primordial conservative condition. The practice of nestings into holes has developed from a freely breeding form, and out of the three species of tits, the marsh tits have preserved this original condition strongest in their way of life. The great and blue tits adhere to the covered holes offering safer nesting possibilities, they have broken away from the primordial practice of nesting into uncovered open holes which meant a risk to the future of the youngs and thus, with their higher values of survival, populated their habitats at a density by far surpassing the one of the marsh tits.

It is in the first place the young birds that are forced by social selection to take pioneering parts, and although these individuals are incapable of competing with the older generations in their original communities, certain of their characteristics make them the most fit of all for the task of occupying new area. It is, namely, the young individuals which endure the changes with the greatest plasticity; they are responsive to the new constellations of stimuli and easily learn the ways of behaviour suiting the new situation. VINCE (1964, 1966) proved by experimental evidence that at young age (up to 7 – 10 months) the birds' ability to learn was much higher than at older ages. This means that it is the young individuals which best meet the ethological conditions of the expansion of the species.

It is a generally known phenomenon that the great tit is one of the most active species, which settles in the big capitals, it appears in considerable numbers in the direct neighbourhood of industrial plants and also makes use of various technical constructions as nesting places. The blue tits rather settle only in larger parks, for the time of breeding they enter the city to a lesser degree. Again, the marsh tits do not nest among urbanized conditions. Doubtlessly, settlement in the town is brought about by a number of ethological causes, still, the social ethological factor has to be stressed as one of the most important conditions in this process. The species, in the communities of which the social expelling effects do not operate, are able to remain in their original ecological environment. This is by what the marsh tits of low density are characterized. Again, the species in the community to occupy more unfavourable ecological areas. This is the way in which the great tit, a bird of higher density gets to the urban areas. These social ethological motivations explain in part why the great tit is a typicas urban species, why the blue tit penetrates into the ecological milieu of the towns but to a moderate extent and why the marsh tit keeps away from it.

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